PHOTOPERIODIC AFTEREFFECTS IN IPOMOEA[1]

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Photoperiodic aftereffects[2] were first observed by Garner and Allard (8) in 1923, and have been studied since then in about two dozen species of plants. Due largely to the extensive studies of Borthwick and Parker (2, 3, 4, 17, 18), we now know more about photoperiodic aftereffects in Biloxi Soy Beans than in any other plant. Photoperiodic aftereffects in soy beans have also been studied by Garner and Allard (8), Eghiz (7), Murneek (15), and others. Considerable work on after-effect in millet has been done by various Russian botanists (5, 6, 14, 23). Photoperiodic aftereffects in chrysanthemum have been studied by Poesch (19), Post (20, 21), and Link (13), in *Xanthium* by Hamner and Bonner (10) and Neidle (16), in dill by Hamner and Naylor (12), and in Klondike Cosmos by Biddulph (1). Other species which have been studied less thoroughly include teosinte, oats, barley, common cosmos, radish, poinsettia, rice, cotton, *Rudbeckia* and spinach. These studies have dealt primarily with reproductive aftereffects, but aftereffects involving tuber formation have been reported in *Solanum* by Razumov (24) and Pushkarev (22) and in *Helianthus tuberosus* by Hamner and Long (11).

In view of the fact that none of these plants has been a vine and that none has belonged to the *Convolvulaceae* the writer considered it worth while to investigate possible photoperiodic aftereffects in *Ipomoea*. The species employed were the Japanese morning glory (*I. hederacea* Jacq.) and the common morning glory (*I. purpurea* Roth.). Both of these species were classified by Garner and Allard (8) as short day plants, although Roberts and Struckmeyer (25) found that the latter species would also bloom under long photoperiods if the temperature was relatively low.

EXPERIMENTAL METHODS

A transfer technique similar to that employed in previous investigations on photoperiodic aftereffects was used. Plants of both species were subjected to from 1 to as many as 20 induction photoperiods of 9 hours each, transfers to long photoperiods being made daily. In the various experiments plants were kept under long photoperiods for different lengths of time before being subjected to the induction treatments, thus securing plants of different ages at the time the treatments were begun. Care was exercised that plants would be subjected to short photoperiods only during the allotted induction periods. Control plants were kept under short photoperiods from the beginning of the treatments to the end of the experiments. Other control plants were retained under long photoperiods throughout the experiments.

The experiments were conducted at Columbus, Ohio, between April 22 and September 3, 1939. The photoperiods designated as long were between 15 and 16¼

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[2]Although the terms *photoperiodic induction* and *photoperiodic aftereffect* are often used synonymously the writer believes that they logically refer to distinct phenomena. As used here the term *photoperiodic induction* is restricted to the initiation of sexual reproduction in plants under the influence of the photoperiod. The term *photoperiodic aftereffect* is applied to the continuation of reproductive development after photoperiods favoring its initiation have been replaced with photoperiods unfavorable or less favorable for induction. The term may also be applied to the continuation of vegetative development characteristic under certain photoperiods after these have been replaced by others under which such development would not initially occur. A detailed discussion of this terminology is given elsewhere (9).

hours in length. These were obtained by using the natural photoperiods, either alone or supplemented with light from Mazda bulbs; these providing a minimum of 3 foot candles of light, although most of the plants received at least 20 foot candles of light. The photoperiods designated as short were 9 hours in length, and were obtained by means of light-proof, ventilated chambers and cabinets. The temperature differences between the inside and outside of these were not great enough to have any significant effect on the development of the plants. The minimum temperature to which any of the plants was exposed was 56° F., and for short periods only. The mean temperatures ranged between 70° F. and 80° F.

The plants were maintained in five-inch porous clay pots according to good greenhouse practice, and care was taken to keep such factors as soil, moisture and light intensity as uniform as possible.

TABLE I

DATA ON THE ORGANIZATION OF THE EXPERIMENTS

SPECIES	EXPT. NO.	DATE PLANTED	NUMBER OF DAYS FROM PLANTING SEEDS TO THE:			PLANTS PER TREATMENT
			Beginning of Treatments	Time of the Last Transfer	End of the Experiment	
I. hederacea..... (yellow-green)	I	April 21	40	60	96	2
" "	II	June 13	4	21	62	3
I. hederacea..... (dark green)	III	June 29	5	18	66	4
" "	IVa	June 29	28	38	66	4
" "	IVb	June 29	28	41	66	3
I. purpurea.....	I	April 21	40	60	96	3
" "	II	June 13	4	22	66	4
" "	III	June 29	5	22	66	3
" "	IV	June 29	28	45	66	3

Eight different experiments were conducted, four on each species. In the first two experiments on *I. hederacea* a strain with pale yellow-green foliage was used, while in the last two a strain with dark green pigmentation, similar to that of *I. purpurea*, was employed.

In Experiment IV on *I. hederacea* the plants were divided into two series, *a* and *b*. The plants in Series *a* were treated in the usual way, but the plants in Series *b* had only one leaf each exposed to nine hour photoperiods. This was accomplished by means of light-proof black cloth bags placed in position and removed daily.

Daily records were made of the development of the plants, including a complete record of anthesis, and at the close of each experiment the height of each plant was measured and the number of fruits on each was counted. All plants which had not bloomed were carefully examined for flower buds with a low power binocular

microscope. Specific details about the organization of the experiments are given in Table I.

RESULTS AND DISCUSSION

Detailed data on each of the experiments are too extensive to present here but are available elsewhere (9). It will suffice here to describe and discuss the more important results, considering in turn the aftereffects related to flower bud formation, anthesis, and fruit formation.

Flower buds developed on at least some of the plants in all the treatment groups in the experiments on *I. hederacea* (Table II), and in the first three experiments flower buds were also present on the control plants, which were retained under photoperiods 15 hours or more in length throughout the experiments. However, the influence of the short day treatments was clearly evident, as the buds on

TABLE II

MINIMUM NUMBERS OF SHORT PHOTOPERIODS WHICH INDUCED VARIOUS AFTEREFFECTS

EXPERIMENT	MINIMUM NUMBERS OF SHORT PHOTOPERIODS WHICH INDUCED					
	Flower Buds	Terminal Flower Buds	Anthesis	First Anthesis	Last Initial Anthesis	Fruit Formation
Ipomoea hederacea I	0	2	0	12	0	0
" " II	0	2	2	11	2	2
" " III	0	5	5	13	5	5
" " IVa	1	7	3	7	3	6
" " IVb	1	11	4	9	4	13
Ipomoea purpurea I	2	8	3	4	3	4
" " II	7	13	7	10, 11, 14, 16, 17	12	13
" " III	11	12	11	7	11, 12	12
" " IV	2	17	8	14, 15	9	17

the control plants appeared much later than on the treated plants, and in no case before the plants were 46 days old. None of the *I. purpurea* plants exposed to less than 2 short photoperiods formed flower buds, and in Experiments II and III on this species flower buds appeared only on plants exposed to 7 or more and 11 or more short photoperiods respectively. Since treatments were begun in these experiments 4 and 5 days respectively after planting, and were not begun until 40 and 28 days after planting in the other two experiments, it appears that induction treatments may be more effective in inducing flower bud formation when applied to older plants. The formation of flower buds on the control plants of *I. hederacea* indicates that this is less strictly a short day species than *I. purpurea*.

More short photoperiods were necessary for the induction of terminal flower buds than lateral flower buds (Table II). The yellow-green plants of *I. hederacea* were most sensitive in this respect, terminal flower buds developing on some of

the plants exposed to 2 to 4 short photoperiods, and on all the plants exposed to 5 or more short photoperiods. Terminal flower bud formation was much less extensive in the dark green plants of this species, being present only in scattered plants exposed to 5 or more short photoperiods. A terminal flower bud formed on only one of the plants subjected to localized induction photoperiods, it having been exposed to 11 short photoperiods.

In *I. purpurea* terminal flower buds were also rare, and except in the first experiment occurred only on scattered plants exposed to 12 or more short photoperiods. In the first experiment terminal flower buds formed on one plant each in the groups exposed to 8, 9, 10, and 14 short photoperiods and on all plants exposed to 15 or more short photoperiods. The greater abundance of terminal flower buds on these plants was probably due in part to the greater age of the plants at the time the treatments were begun, and in part to the fact that this experiment was continued a month longer than the other experiments on *I. purpurea*. Terminal flower buds formed on all plants of both species which were retained under short photoperiods from the beginning of the treatments to the ends of the experiments. Most of the terminal flower buds developed into flowers, but a few on the plants subjected to the lesser number of short photoperiods failed to develop further.

A very striking result of the formation of terminal flower buds was a cessation of growth of the main axis and the consequent dwarfing of the plants (Fig. 1). In some of the plants exposed to fewer numbers of short photoperiods branches continued to grow and one exhibited apical dominance. The resulting plant as a whole had the usual viny form, but in most of the plants terminal flower buds soon formed on the branches, resulting in a bushy plant entirely unlike the usual morning glory plant. It is possible that non-viny *Convolvulaceae*, such as *Convolvulus tricolor*, are bushy because their terminal flower buds develop under longer photoperiods than in other members of the family.

The average height of the dwarfed plants was 30 cm. for the plants treated beginning 4 or 5 days after planting and 118 cm. for those treated when older. The yellow-green plants of *I. hederacea* averaged the shortest, followed in order by the dark green plants of this species and the *I. purpurea* plants. In all but one experiment (*I. purpurea*, Expt. III) the plants retained under short photoperiods were shorter on the average than the plants returned to long photoperiods after induction, apparently because of the continued influence of the short photoperiods. No explanation for the exception is evident. However, formation of terminal flower buds did not necessarily occur earlier with an increase in the number of induction photoperiods, many plants exposed to the larger numbers of short photoperiods having main stems averaging about the same in height as those on which terminal flower buds developed after exposure to as few as 2 short photoperiods. The shortest main stems were those of two plants of *I. hederacea* in Experiment I which had been exposed to 15 and 16 short days and were only 8 cm. tall.

In general, extensive branching accompanied the formation of terminal flower buds, probably as a result of the loss of apical dominance, and branching was rare in plants with terminal vegetative buds. For example, in Experiment I on *I. hederacea* 78 per cent of the plants had terminal flower buds and 71 per cent had branches, while in Experiment III on this species only 8 per cent had terminal flower buds and none had branches. When plants with terminal flower buds failed to branch, as was evident particularly in Experiment II on *I. hederacea*, in which 78 per cent of the plants had terminal flower buds but only eight per cent had branches, it was evidently because all the axillary buds had developed into flower buds so that no further stem elongation was possible.

In Experiment I on *I. hederacea* the control plants kept under long photoperiods began blooming 85 days after planting. None of the control plants in the other

experiments bloomed, although some of the *I. hederacea* controls which had flower buds might have bloomed had the experiments been continued longer. In these experiments the minimum number of short photoperiods necessary to induce anthesis ranged from 2 to 5, and in *I. purpurea* from 3 to 11 (Table II). Using this as a criterion *I. hederacea* may be considered as more sensitive to photoperiodic induction than *I. purpurea*, and the yellow-green strain of the former species as more sensitive than the dark green strain.

Aftereffects were much more pronounced in the yellow-green plants of *I. hederacea* than in the dark green plants of either species insofar as abundance of bloom is concerned, and flowers were more abundant on the dark green plants of *I. hederacea* than on the *I. purpurea* plants. There was a general tendency for the

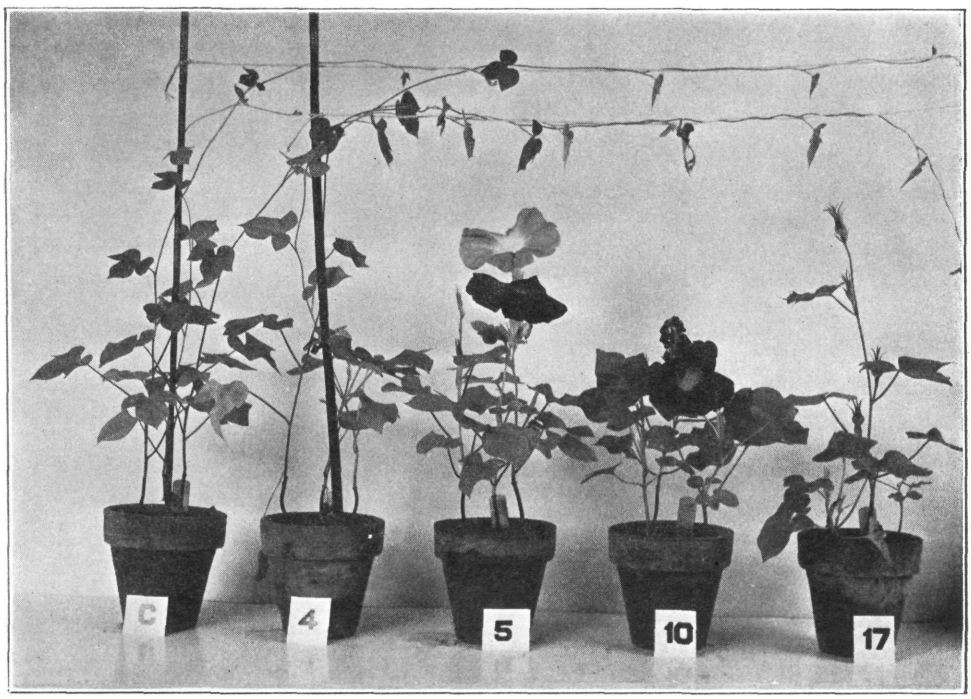

Fig. 1. Representative plants of *Ipomoea hederacea*, Experiment II, showing the dwarfing which resulted from the conversion of the terminal bud to the determinate reproductive condition. The figures give the number of short photoperiods to which the plants were exposed. The plant labeled "C" was retained under long photoperiods throughout the experiment. Photographed July 31, 1939.

plants exposed to greater numbers of short photoperiods to bloom more abundantly than those exposed to smaller numbers, but there was no regular increase in abundance of bloom with an increase in the number of induction photoperiods. All plants retained under short photoperiods bloomed much more abundantly than those returned to long photoperiods. There was no distinct correlation between either the abundance of bloom or the minimum number of short photoperiods necessary to induce anthesis and the age of the plants at the time the treatments were begun.

In *I. hederacea* anthesis first occurred in plants exposed to a fairly large number of short photoperiods, and the last plants to begin blooming were ones exposed

to only a few short photoperiods, but this was not true of *I. purpurea* (Table II). Anthesis first began in the plants retained under short photoperiods from the beginning of the treatments at about the same time as in the plants returned to long photoperiods (Table III). Both the time of initial anthesis and the beginning of the period of maximum anthesis correlated with the number of days from the beginning of the treatments rather than with the number of days from planting (Table III). The time from the beginning of the treatments to the first anthesis varied from 21 to 30 days and the time to the beginning of maximum anthesis varied from 25 to 30 days. That the treatments were somewhat more effective on plants which were older at the beginning of the treatments is indicated by the fact that the average time from the beginning of the treatments to initial anthesis was 24 days for the older plants and 29 days for the younger plants. The average time to the beginning of maximum anthesis was 28 and 30 days respectively. There was little difference between the two species or between the yellow-green and dark green plants in the time required for initial and maximum anthesis to begin.

The number of short photoperiods necessary for the induction of fruit formation was about the same as that for the initiation of terminal flower buds (Table II), and except in the first three experiments on *I. hederacea* was greater than the number required for inducing anthesis. Fewer numbers of short photoperiods were necessary in both strains of *I. hederacea* than in *I. purpurea*, except in the plants of which single leaves were exposed to localized short photoperiods. The percentage of the test plants bearing fruits was markedly higher in *I. hederacea* than in the comparable experiments on *I. purpurea*, except in Experiment I on each species, where the longer duration of the experiments may have made some equalization possible, and in the plants given localized short photoperiods, only 5 per cent of which formed fruits. In Experiment I, fruits developed on 73 per cent of the *I. hederacea* plants and on 61 per cent of the *I. purpurea* plants. In Experiments 2, 3, and 4 the percentages were 61 and 13, 24, and 7, and 40 and 2 for *I. hederacea* and *I. purpurea* respectively. Fruits developed on 77 per cent of the plants retained under short photoperiods. The percentage of flowers developing into fruits was extremely variable from treatment to treatment and there was no correlation with the number of short photoperiods or the species, but it was higher in the plants retained under short photoperiods than those returned to long photoperiods.

Photoperiodic aftereffects were evident in the plants of *I. hederacea* which had only one leaf each exposed to short photoperiods (Exp. IV b), but these were much less extensive than in comparable plants exposed in their entirety to short photoperiods (Exp. IV a). Flower buds formed on a plant exposed to only one localized short photoperiod, anthesis occurred on plants exposed to 4 or more localized short photoperiods except in the groups exposed to 5 and 10 short photoperiods, and fruits formed on one plant exposed to 13 localized short photoperiods. A terminal flower bud developed on one plant exposed to 11 localized short photoperiods when it was 101 cm. high.

The various tabulations fail to indicate adequately the rather marked differences in development among plants receiving identical treatments. These differences of reaction to the photoperiod were in many cases too marked to be due to other slight differences in environment and it appears that individual hereditary differences in reaction to the photoperiod are greater within ordinary unselected species than is generally recognized.

The more pronounced photoperiodic aftereffects of the yellow-green strain of *I. hederacea* than of the dark green strain may have been due either to genetic linkage of the factors affecting sensitivity to the photoperiod and the factors affecting pigment formation, or to a more or less direct physiological connection between pigmentation and sensitivity to the photoperiod. The latter appears

possible since Murneek (15) found that in several short day plants the carotene and xanthophyll content was higher in plants growing under short photoperiods than those growing under long photoperiods.

A quantitative and cumulative relationship between exposure to short photoperiods and photoperiodic aftereffects was indicated by the following results: a general increase in photoperiodic aftereffects with an increase in the number of short photoperiods to which the plants were exposed; more extensive reproductive development in plants retained under short photoperiods than in those returned to long photoperiods; and the lesser aftereffects in *I. hederacea* plants exposed to localized short photoperiods than in comparable plants exposed in their entirety to short photoperiods. These results are in accord with the florigen theory.

TABLE III

LENGTHS OF TIME FROM PLANTING AND BEGINNING OF TREATMENTS TO THE INITIATION OF ANTHESIS

EXPERIMENT	NUMBER OF DAYS FROM PLANTING TO:				NUMBER OF DAYS FROM BEGINNING OF TREATMENTS TO:	
	Beginning of Treatments	First Anthesis of		Period of Maximum Anthesis	First Anthesis	Beginning of Maximum Anthesis
		Test Plants	Short Day Plants			
Ipomoea hederacea I	40	64	..	70–80	24	30
" " II	4	31	..	35–41	27	31
" " III	5	35	36	36–43	30	31
" " IVa	28	54	52	56–66	26	28
" " IVb	28	56	52	56–66	28	28
Ipomoea purpurea I	40	61	..	65–80	21	25
" " II	4	34	35	34–40 58–62	30	30
" " III	5	33	36	34–37	28	29
" " IV	28	51	51	55–62	23	28

SUMMARY

Plants of *Ipomoea hederacea* and *I. purpurea* exhibited photoperiodic aftereffects in various degrees when transferred to long photoperiods after having been exposed to various numbers of 9 hour photoperiods. In general, more short photoperiods were necessary to induce anthesis than flower bud formation, and still more to induce fruit formation. The photoperiodic aftereffects were generally more pronounced with an increase in the number of short photoperiods to which the plants were exposed and with an increase in the age of the plants at the time the treatments were begun, but reproductive development was not as extensive in the transfer plants as in those retained under short photoperiods from the beginning of the treatments to the end of the experiments.

A pale yellow-green strain of *I. hederacea* exhibited more marked photoperiodic aftereffects than plants of the dark green strain of this species, and the aftereffects in *I. purpurea* were less marked than in either strain of *I. hederacea.*

Except in one experiment, flower buds developed on plants of *I. hederacea* retained under long photoperiods, indicating that this species is not strictly a short day plant, although the added influence of the short day treatments was clearly evident. In *I. purpurea* flower buds developed only on plants exposed to 2 or more short photoperiods.

Terminal flower bud formation occurred only after exposure to minima of from 2 to 7 short photoperiods in *I. hederacea* and 8 to 17 short photoperiods in *I. purpurea,* and was much more frequent in the former. This resulted in the formation of dwarf plants, many of which were bushy and some of which had main stems as short as 8 cm. The plants on which experiments were begun when they were very young were shorter than those on which treatments were begun later. Branching was in general more extensive on the plants with terminal flower buds, but some of these did not branch because all lateral buds had developed into flower buds.

The minimum number of short photoperiods which induced anthesis in *I. purpurea* was 3 and the minimum in *I. hederacea* was 2, except that in one experiment on the yellow-green strain of the latter species even the plants retained under long photoperiods bloomed. Anthesis began in from 21 to 30 days after the beginning of the treatments. Initial anthesis occurred about the same time in some of the transfer plants as in those retained under short photoperiods. The number of short photoperiods necessary for induction of fruit formation was about the same as that for the initiation of terminal flower buds.

Plants of the dark green strain of *I. hederacea* exhibited photoperiodic aftereffects after the application of localized short photoperiods to one leaf, but these aftereffects were much less marked than those in comparable plants exposed in their entirety to short photoperiods.

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